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MADROÑO

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NOTES ON THE PHACELIA MAGELLANICA COMPLEX IN THE PACIFIC NORTHWEST

A. R. KRUCKEBERG[1]

The members of the *Phacelia magellanica* complex (Hydrophyllaceae) have defied satisfactory taxonomic delimitation ever since the traditional linneon of *P. circinata* Jacq. was found inadequate by E. L. Greene and later workers (Brand, 1913 and Macbride, 1917). Recently Cave and Constance (1942, 1944, 1947, and 1950) and Heckard (1954) have indicated the probable basis for the lack of clear-cut boundaries between the members of the group. After having made chromosome counts on a large number of field collections, it became evident to Cave and Constance that the taxa comprising this assemblage are elements of a polyploid complex. The intricate pattern of apparently reticulate phylogeny in the group has not as yet been transformed into a workable taxonomic scheme. A part of the taxonomic elucidation awaits the accumulation of additional cytological information on collections from areas in the west where phacelias have not been intensively collected. The Pacific Northwest is one such area. The present paper reports on field studies and chromosome counts of phacelias from northwestern United States and western Canada. A new diploid is described from Oregon and, for the first time, the existence of hexaploids in the complex is recorded.

I. A NEW PHACELIA FROM SOUTHWESTERN OREGON

Phacelia capitata sp. nov. Herba caespitosa perennis, 10–15 pedunculis tenuibus, quisque ex rosula laterali; pedunculi erecti simplices longi 20–25 cm.; folia rosulata spisse sericea angustato-lanceolata integra longa 2–3 cm., lata 0.2–0.4, sessilia; folia caulina reducta, longa 2–3 cm., lata 0.2–0.4 cm.; inflorescentia ex 2–3 cymis in unico racemo congesto subcapitato constans; racemus cymarum demum longus 2.0–2.5 cm., latus 3.0–3.5 cm.; pedicelli longi 1–3 cm., hispidi; calycis lobi angustato-oblongi longi 3 mm., lati 0.5–0.8 mm., margines pilis longis hispidi; superficies abaxialis pilis brevibus hirsuta; corolla alba rotato-campanulata longa 4–6 mm., lata 3–5 mm., lobi simplices obtuso-rotundati; appendiculae 1 mm. supra basin tubae corollae affixae; stamina et stylus exserta 5–7 mm., filamenta glabra vel paucis pilis sparsis; capsula immatura ovoidea longa 2–3 mm. tecta setis robustis longis 2–3 mm crebe; semina non visa.

Deeply taprooted cespitose perennial with 10–15 thin, wiry peduncles arising from as many rosulate tufts, the whole forming a broad and multicipital rosette, 25–30 cm. in diameter; stems erect, unbranched, 20–25 cm. tall, finely sericeous; silvery-gray herbage consisting of a hyaline-

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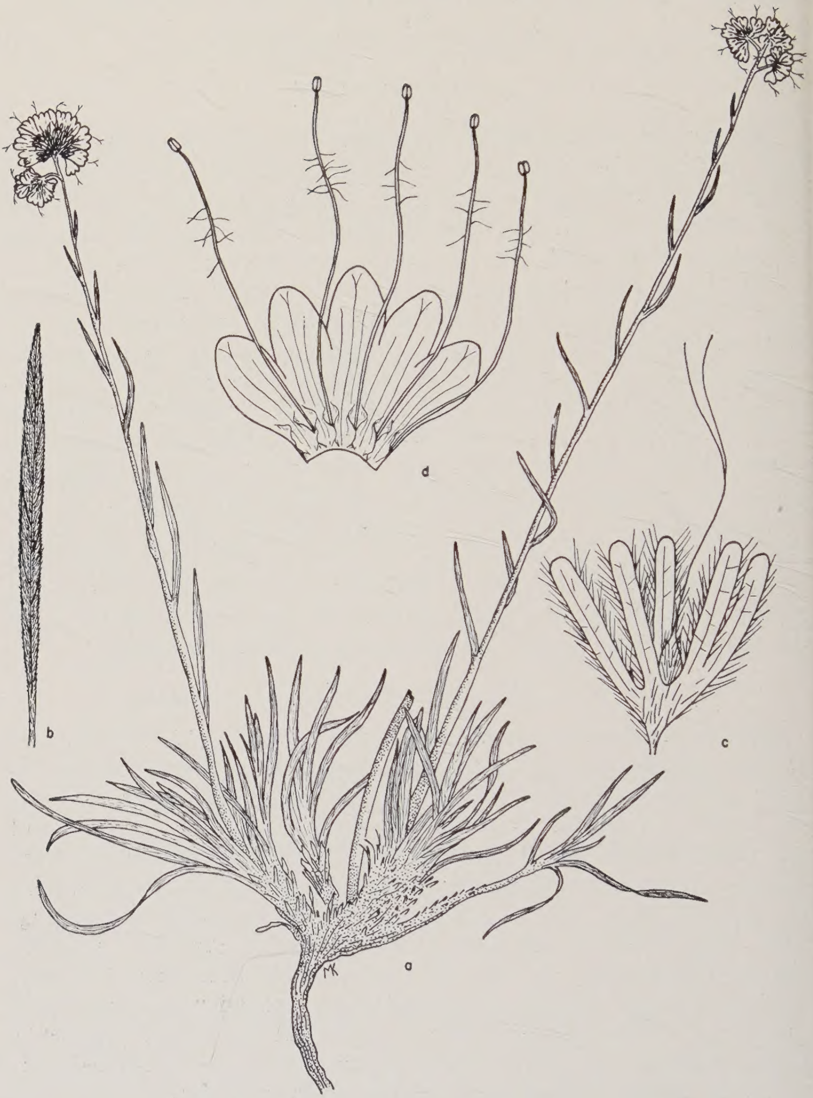

FIG. 1. *Phacelia capitata* sp. nov. *a,* habit; *b,* basal leaf; *c,* flowering calyx; *d,* expanded corolla. (Habit drawing × 2/5; leaf × 4/5; calyx and corolla × 6.)

shiny pubescence of two sorts: appressed bristles on a background of thinly matted hairs; basal leaves linear-lanceolate, simple, entire, 2–3 cm. long, 0.2–0.4 cm. wide, apparently sessile; the 8–12 cauline leaves gradually but not wholly reduced, 0.7–2.0 cm. long, 0.2–0.4 cm. wide; inflorescence consisting of 2–3 scorpioid cymes in a congested, subcapitate erect cluster, 2.0–2.5 cm. long and 3.0–3.5 cm. wide in early fruit, that is usually borne singly and terminally and subtended by much reduced cauline leaves; pedicels in early fruit 1–3 mm. long, hispid; calyx lobes linear-oblong, 3 mm. long, 0.5–0.8 mm. wide, two-thirds as long as corolla, margins long-hispid, abaxial surface short-hirsute; corolla white, rotate-campanulate, 4–6 mm. long, 3–5 mm. broad, the lobes entire, obtuse-rounded; appendages attached barely a millimeter above the base of the corolla tube, the free portions forming a long (3 mm.) and narrow "V" distally; stamens and style exserted 5–7 mm., the filaments glabrous or with a few scattered hairs about mid-length along the filament; immature capsule ovoid, 2–3 mm. long, densely clothed with stout bristles 2 mm. long; mature seeds not seen; $n = 11$ (chromosome count from buds of type collection).

Type. On serpentine roadcut, 2 miles east of Bridge, above Coquille River and along State Highway 42, Coos County, Oregon, May 31, 1951, *A. R. Kruckeberg 2703* (WTU No. 153940). Growing with *Cheilanthes siliquosa, Sisyrinchium bellum, Eriophyllum lanatum* and *Eriogonum nudum*. Topotypes: ⅛ mile north of State Highway 42, *Kruckeberg 3313;* "stony slope near Bridge, *M. E. Peck 20324* (UC); *C. L. Hitchcock s. n.* (specimen from field transplant grown in greenhouse); 2.5 miles east of Bridge, *Constance 3454* (seedlings also grown in greenhouse, *Heckard S-295,* UC). Other collections seen. OREGON. Serpentine bluff about 1 mile northerly from Myrtle Creek, *J. T. Howell 28807* (CAS); 2 miles south of Myrtle Creek, *Eastwood and Howell 1474* (CAS).

Phacelia capitata is distinguished from its nearest congeners by a number of features which are summarized in Table 1.

In addition to the features just tabulated, there are three others that give this new taxon specific distinction: (1) The large number of thin, wiry stems arising from the broadly cespitose rosettes; (2) the large number of cauline leaves; (3) the rarity of cymes below those of the terminal capitate cluster. Some of these diagnostic characters are illustrated in figure 1. The distinctness of *P. capitata* is further enhanced by its diploid chromosome complement. To date, only one other diploid collection of a *magellanica*-type *Phacelia* has been reported for Oregon (Cave and Constance, 1942). This, the wide-ranging, rank biennial, *P. heterophylla* Pursh, is a very different entity.

A search through herbarium material collected in southwestern Oregon which was available from several western herbaria has failed to disclose additional specimens that closely match those from the type locality of *P. capitata*. A specimen collected at Reston, Douglas County, by Professor Morton E. Peck (*Peck 6035* WILLU) is suggestive of the new species, but differs in having tawny-green herbage, wider basal leaves and fewer cauline leaves. Collections from the Roseburg-Myrtle Creek area in Douglas County resemble *P. capitata: Peck 6033, 6022* (WILLU);

TABLE 1. COMPARISON OF PHACELIA CAPITATA WITH NEAREST CONGENERS

Species	n number	Color and vesture of herbage	Length of leaves		Shape and lobing of leaves	Kind of inflorescence	Range and habitat
			Basal	Cauline			
capitata	11	Silvery-gray, eglandular, appressed-hispid.	2–3 cm.	0.7–2 cm.	Linear-lanceolate, entire.	Capitate cluster of 2–3 cymes; tall, stiffly erect.	Dry, serpentine outcrops. Known only from type locality, Coos Co., Oregon.
corymbosa	11, 22	Tawny-ferrugineous cast; glandular-hispid	2–7 cm.	2–3 cm.	Linear to lance-oblong, often with 1–2 pairs of leaflets at base of lamina.	Cymes in dense or open corymbs; stems 15–35 cm. tall, ascending.	Dry serpentine and peridotite outcrops. North Coast Ranges from California to southwest Oregon.
leucophylla	22	Silvery-gray, strigose-sericeous	11–15 cm.	8–11 cm.	Lanceolate, entire or rarely with 1–3 leaflets.	Paniculately disposed cymes, peduncle erect or ascending, often branching below terminal cymes.	Open sagebrush or yellow pine areas east of Cascade-Sierran axis from British Columbia south to California and east to Rocky Mountains.

Eastwood and *Howell 1475* (CAS); *Constance* and *Rollins 2966,* and *Cusick 4048* (both WS). Like the new species, the Roseburg-Myrtle Creek specimens have silvery-sericeous foliage and narrowly lanceolate cauline leaves. However, these five specimens do not have the capitate inflorescence or the thin wiry peduncles of *P. capitata.* A further difference is that the plant collected by Constance and Rollins proved to be tetraploid. Constance, at one time, annotated two of the four specimens in question as *P. leucophylla* Torr., thus placing them in a species, the usual distributional limits of which are east across the Cascade Range from Roseburg.

An exploratory search for additional stations of *P. capitata* in the region of the type locality as well as along the south fork of the Coquille River was unrewarding. More intensive botanizing on the serpentine areas of southern Coos County and western Douglas County as well as on similar ecologic sites along the northern boundaries of Curry and Josephine counties may yield new locations.

II. The Hexaploid Phacelia leptosepala Rydberg

A widely accepted practice among field collectors and herbarium workers is to designate as either *Phacelia leucophylla* Torr. or *P. heterophylla* Pursh, those perennial phacelias of the *magellanica* complex that are collected from the crest of the Cascade Range eastward. This practice, at least, has the merit of correctly disposing of the majority of perennial phacelias collected in the Pacific Northwest, for these two taxa are certainly the two most widespread of the complex in the region. Ranging from arid sagebrush plains to the mid-montane pine belt, the two species present a variety of altitudinal and habitat forms. *Phacelia leucophylla* is tetraploid ($n = 22$) in the several widely separated localities of the Pacific Northwest for which chromosomal numbers have been determined (Table 2 and Cave and Constance, loc. cit.). The equally distinctive and ubiquitous *P. heterophylla* is both diploid ($n = 11$) and tetraploid ($n = 22$) throughout the same general range. The more puzzling collections from the Pacific Northwest have been, however, the several high-montane forms of the *P. magellanica* group. Some of these truly appear to be altitudinal races of the two aforementioned taxa, but others are definitely distinct. These montane forms have gone under a variety of names. One of the names in the *P. magellanica* complex recognized as possibly valid by Constance (in Abrams, 1951) is *P. leptosepala* Rydberg. Justification for including within this taxon many of the subalpine collections of *Phacelia* from the Pacific Northwest now will be considered.

Because of the tawny-green herbage, plants considered by the author to be *P. leptosepala* often have been placed under *P. nemoralis* Greene ($n = 11, 22$) a much taller, rank perennial of the Coast Ranges and bordering valleys having one to few stiffly erect stems clothed with strongly hispid-hirsute herbage. The montane plant in question, however, is ces-

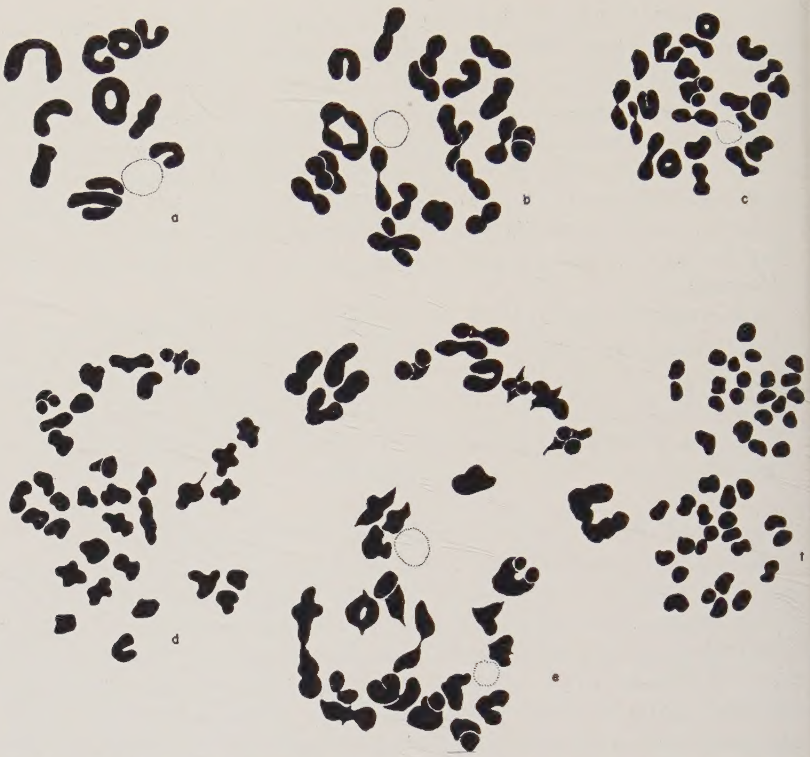

FIG. 2. Meiotic chromosomes in pollen mother cells of certain members of the *Phacelia magellanica* complex. *a, P. capitata,* n = 11 (Diak.), *Kruckeberg 2803*; *b. P. corymbosa,* n = 22 (Diak.), *Kruckeberg S–110*; *c. P. frigida,* n = 22 (Diak.), *Kruckeberg s.n.,* July 1951; *d, P. frigida,* n = 33 (M_I) *Kruckeberg 3781*; *e, P. leptosepala,* n = 33 (Diak.) *Kruckeberg s.n.,* July 1951; *f. P. mutabilis,* n = 22 (M_{II}), *Kruckeberg 3779.*

pitose, with several assurgent to erect flowering stems. This discrepancy led Jones (1936) in his treatment of the flora of the Olympic Peninsula to remark: "the lowland plants are erect, 60–180 cm. tall, strongly hispid-hirsute and probably represent true *P. nemoralis;* the subalpine plants are decumbent at the base, less harshly pubescent, with whiter corollas, and may represent an undescribed species or variety." That Jones' conjecture about the "un-nemoraloid" character of these subalpine plants was a valid one may be judged from an examination of the following evidence.

During the past four years, numerous collections of bud samples for chromosome counts, as well as of living plants and herbarium specimens have provided information which permits a better understanding of this puzzling *Phacelia.* Very soon it was discovered that all tawny-leaved, cespitose plants collected in the Cascade and Olympic ranges of Wash-

TABLE 2. HAPLOID CHROMOSOME NUMBERS OF NORTHWEST PHACELIAS

	Haploid Chromosome Number	Number of Collections
P. capitata Kruckeberg	11*	3
P. corymbosa Jepson	(11)†, 22	2
P. frigida Greene	22, 33*	7, 3
P. heterophylla Pursh	11, (22)	1
P. leptosepala Rydberg	33*	18
P. leucophylla Torrey	22	14
P. mutabilis Greene	(11), 22	5
P. nemoralis Greene	(11), 22	2

* Hitherto unreported chromosome numbers; other numbers confirm counts by Cave and Constance (*loc. cit.*).

† Haploid numbers in parentheses are from Cave and Constance (*loc. cit.*).

ington were hexaploid (n = 33, see fig. 2e and Table 2). Moreover, the chromosome number, n = 33, could be predicted with considerable accuracy in all subsequent collections that were "leptosepaloid" in character. This record of a hexaploid is the first for any *Phacelia*. The type of *P. leptosepala* from Vermilion Lake, British Columbia, as well as the three other specimens from British Columbia and Montana cited by Rydberg (1909) have been examined and prove to be good matches for the hexaploid material from Washington. Unfortunately, it has not yet been possible to obtain material for chromosome counts on the phacelias from the type locality.

Despite the apparently extensive range of *P. leptosepala* throughout the Pacific Northwest, it has not been collected at all frequently. Only 102 specimens out of over 800 sheets of the *P. magellanica* complex from the Pacific Northwest on loan from ten herbaria were judged by the author to be *P. leptosepala*. This scarcity is perhaps easily understood in view of the likelihood that, in its superficial resemblance to montane forms of *P. leucophylla* and *P. heterophylla*, it might be regarded as too common to be collected.

Phacelia leptosepala is perhaps more like *P. corymbosa* Jepson than any other of the possible congeners in the Northwest. Both are cespitose and have a ferrugineous cast to the herbage. However, *P. corymbosa* is distinguished from *P. leptosepala* in the possession of a decidedly glandular pubescence. Moreover, it has been collected thus far as either a diploid or a tetraploid and may be separable from *P. leptosepala* on chromosome number. The two species are widely disjunct in distribution, *P. corymbosa* being confined rather closely to the serpentines of southwestern Oregon and northern California.

Phacelia mutabilis Greene (n = 11 and n = 22) and *P. leptosepala* may in exceptional specimens bear close resemblance to each other. In typical material, however, *P. mutabilis,* with its weakly rosulate habit and few short and erect or assurgent stems is readily distinguishable from *P. leptosepala.* In mid-montane areas of the Cascade Range of southern Washington, *P. nemoralis* and *P. leptosepala* may intergrade. In the excellent series of phacelias collected by Suksdorf around Mount Adams (Mount Paddo) are certain specimens which cannot be placed readily in either *P. leptosepala* or *P. nemoralis.* The mid-montane populations in the Mount Adams-Skamania County area may truly represent altitudinal variants of *P. nemoralis.* Data on recent collections from this area are noteworthy. One from Spirit Lake (*Kruckeberg 3814*) was tetraploid; the plants are like those collected by Suksdorf, and may thus be regarded as samples of a mid-montane ecotype of *P. nemoralis.* Two collections were made on the nearby slopes of Mt. St. Helens, possibly four air-line miles away and 1000 feet higher; both were hexaploid and "good" *P. leptosepala.* When additional collections from this area have been examined cytologically, it should be possible to make a better evaluation of the phacelias in the territory of Suksdorf's most intensive collecting.

A number of characters distinguish *P. leucophylla,* typically an inhabitant of the sagebrush and yellow-pine belt, from *P. leptosepala.* Differences between them have been compiled in Table 3. Equally separable from *P. leptosepala* is the lavender-flowered high-montane, *P. leucophylla* var. *alpina* (Rydb.) Dundas. Although *P. alpina* Rydberg has been considered an infra-specific element of the biennial, *P. heterophylla* Pursh, because of its greater similarity to *P. leucophylla* in habit, leaf shape and vesture, and flower color, the author agrees with both Dundas (1933) and Macbride (1917) that it had best be considered an altitudinal variant of the latter species. Like *P. leucophylla,* var. *alpina* has whitish, sericeous herbage and mostly simple leaves, it may be expected to be sympatric with *P. leptosepala* in eastern British Columbia, Montana, and Idaho. Less tangible are the morphological differences between *P. leptosepala* and *P. frigida* Greene, the latter from subalpine regions in the southern Cascades of Oregon and in the Sierra Nevada of California. Typically, the more diminutive *P. frigida* is not obviously ferrugineous-green, but merely sericeous or anthocyanous-gray in foliage. Though the range of *P. frigida* is mainly to the south of that for *P. leptosepala,* occasional specimens from more northerly areas of the Oregon Cascades cannot be clearly distinguished from dwarfed specimens of *P. leptosepala* collected in the northern Cascades or Olympics of Washington. Of two such specimens seen, one came from Nash Crater lava flows, Linn County (*A. W. Roach s.n.,* OSC) and the other from Three Fingered Jack, Jefferson County (*Constance 3444,* UC). The latter proved to be tetraploid (fide Constance, personal comm.). Thus in Oregon the ranges of the two may well overlap. Even with more typical material, *P. leptosepala* and *P. frigida* cannot be clearly separated on the basis of chromosome number. Seven collections of "good" *P. frigida* were determined by Cave and Constance

TABLE 3. MORPHOLOGICAL COMPARISON OF P. LEPTOSEPALA AND P. LEUCOPHYLLA

	P. leptosepala	*P. leucophylla*
HABIT	Cespitose, flowering stems usually procumbent to assurgent, with many basal subrosettes; caudex with numerous branches either bearing stems or sterile rosulate shoots. Herbage tawny-ferrugineous throughout with mainly hirsute-hispid pubescence.	Flowering stems mainly erect from single or a few tufts of rosette leaves. Foliage silvery-canescent throughout, clothed with mixed strigose and sericeous pubescence.
STEMS	Several, decumbent to assurgent.	1–3, assurgent to stiffly erect.
BASAL LEAVES	9–11 cm. long, 7–10 mm. wide, occasionally entire or usually with 3–5 leaflets, petiole 4 cm. long; lanceolate in outline; long-hispid mainly on veins and margin of blade, sparingly hispidulose in intercostal areas; pungent bristles usually reddish brown.	11–15 cm. long, 1–1.5 cm. wide, commonly entire or rarely with 1–3 leaflets, petiole 4–10 cm. long; strigose mainly on margins and veins, densely sericeous on intercostal areas of lamina. Hairs of pubescence always glistening white.
CAULINE LEAVES	Several, somewhat reduced, compound, with 3 leaflets, 5–8 cm. long, hispid.	Numerous, scarcely reduced except just at base of cymes, mainly entire, 8–11 cm. long, strigose-sericeous.
INFLORESCENCE	Flowers at anthesis in dense, tightly coiled cymes in corymbs, the cymes 4–5 cm. long, tawny-hispid throughout.	Flowers at anthesis in virgately disposed cymes, the cymes 6–8 cm. long, straight except for tight coil of unopened flowers at tip, silvery strigose-hispid throughout.
CALYX	Lobes at anthesis linear-lanceolate, 9 by 1.0 mm.; long, stiff, pungent bristles mostly scattered on margin and on faint midrib; short soft hairs thinly scattered over lamina of lobe.	Lobes at anthesis ovate-lanceolate, 6 by 1.5 mm.; long stiff, pungent bristles on margin and scattered on abaxial surface, short-pilose hairs intermixed on lamina of lobe.
COROLLA	Tubular-campanulate, 7 mm. long, exserted.	Rotate-campanulate, 5 mm. long, 5 mm. broad.
STAMENS	Filaments pilose, 8–9 mm. long, exserted.	Filaments pilose, 10–12 mm. long, exserted.
PISTIL	Style 9 mm. long, bifid to ½ its length, hispidulose at base; capsule hispid.	Style 12 mm. long, bifid to ⅓ its length; hispidulose at base, capsule hispid.
SEED	Lance-ovate, 2–3 mm. long, brown, reticulate-pitted on all faces.	Ovate (to lance-ovate), 2.0–2.5 mm. long, brown to black, reticulate-pitted on all faces.
DISTRIBUTION	Montane and subalpine regions of Cascades and Olympic ranges of Washington; mountains of British Columbia and east along Canadian border to Rocky Mountains of British Columbia, Alberta, and Montana.	Open sagebrush or yellow-pine areas mainly east of the Cascade-Sierran axis from British Columbia south to California and east to Wyoming, Nebraska, and Colorado.

(personal comm.) as tetraploid. Yet of the four cytological samples of typical *P. frigida* taken by the author, only one was tetraploid; the others were hexaploid (i.e., like *P. leptosepala*). A fifth hexaploid collection of *P. frigida* was made late in 1955, from Mt. Hood, Oregon (*Kruckeberg 4000*). One hexaploid was from Crater Lake in Oregon and the other two were from Mt. Lassen and the central Sierra Nevada of California. This is an instance where incomplete cytological evidence could have been used to emphasize taxonomic discontinuity, but where additional chromosome numbers make such use of cytological data unwarranted.

Along the eastern flank of the Cascades of Washington, in areas of mid-montane altitudes, *P. leptosepala* and *P. leucophylla* can be expected to occur sympatrically. One such station is on Blewett Pass in Chelan County, where in 1952 the sympatry was positively confirmed by chromosome counts of both tetraploid *P. leucophylla* and hexaploid *P. leptosepala*. The following year a small population sample of ten plants was collected, together with buds, along a roadbank on the southeast-facing side of the pass. All plants appeared to be either good *P. leptosepala* or *P. leptosepala* with a suggestion of "leucophylloid" features. However, every one of the ten plants was hexaploid. It was hoped that the sampling would include both tetraploid and hexaploid plants and possible hybrids between the two different chromosome-numbered populations as well. Examinations of larger population samples would undoubtedly be more effective in judging whether or not these two taxa are interpollinating in this area of contact.

Specimens of Phacelia leptosepala Examined:[2] Oregon. Wallowa County: Evergreen Forest Camp, upper Imnaha River, *Kruckeberg 3315*; upper Toomey Creek near mouth of Imnaha River, *Kruckeberg 2303* (RM); on granitic ridges above Douglas Lake, Wallowa Mountains, *Kruckeberg 2429*.

Washington. Chelan County: Jolly Mountain, *Easton s.n.* (OSC); Falls Creek near Bryan Butte, *Ward 59* (WS); Ice Creek, *Morill 369*; Nelson Butte lookout, *Kelly 28* (WS); Stuart Pass. *St. John* and *Thayer 7308* (WS); Stevens Pass, *Otis 789* (WS). Clallam County: Mount Storm King, *Lawrence 351* (WS); Olympic Mountains, *Elmer 2829* (WS); Mount Angeles, *Kruckeberg 2782, J. W. Thompson 5519, Webster 1109;* ridge trail between Hurricane Ridge and Mount Angeles, *Kruckeberg 3807*; Seven Lakes Basin, *G. N. Jones 8249, 8267*. Garfield County: Bluffs above Tucannon River, near Willow Spring road, *Peters 388B* (WS). Grays Harbor County: Mount Colonel Bob, *Thompson 7284*. Jefferson County: south slope of Mount Constance, *Rollins and Chambers 2649* (UC); Constance Ridge, *G. N. Jones 5803, Meyer 707* (WS); Lake Constance, *Thompson 7902*. Kittitas County: Teanaway-Turnpike Basin trail, *Kruckeberg 2614*; summit of Iron Peak Trail, Teanaway River drainage, *Kruckeberg 3287*; Fish Lake, *Kruckeberg 2954*; divide between Jungle and Johnson Creeks, toward Malcom Mountain, *Hitchcock 19131* (WS); near Naneum Meadows, *Kruckeberg 3247*; Blewett Pass region, *Grant, August 1929*; 1 mile south of Blewett Pass, *Constance* and *Beetle 2758*; head of Beverly Creek, *Thompson 5851*; Bald Mountain, *Thompson 14796* (WS). Lewis County: mica schist peak north of White Pass, *St. John 5631* (WS); Goat Rocks, *Thompson 15219*. Mason County:

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[2] Institutional abbreviations follow Lanjouw and Stafleu, 1952. Specimens for which no herbarium designation is given are from the University of Washington, Seattle.

Skokomish Valley, *Kinkaid s.n.* (WS); Mount Elinor, *Freer 264*; Heart Lake, *Dickinson 26*. Okanogan County: Slate Peak trail, *Kruckeberg 3269*; Cash Creek near Harts Pass, *Kruckeberg 3271*; 2 miles below Mazama, *Kruckeberg 3272*. Pierce County: Chinook Pass Highway, 3 miles west of Ohanapecosh Junction, *Kruckeberg 3803*; Mount Rainier, *C. V. Piper 486*; *Grant, August 1925*; Cowlitz Glacier, *Pope, August 1904*; Mount Wow, *Warren 1606*; Nisqually River at Nisqually Glacier, *Heller 14762*; Carbon River, *Thompson 5446*; Nisqually Checking Station, *Abrams 9213*; below Carbon Glacier, *Eide s.n.* (WS); White River, *Warren 1456* (WS); north side Mount Rainier, *Jones 77* (WS). Skamania County: Mount St. Helens, *Thompson 12673*; Dog Creek, *Suksdorf 11483* (WS); Butterfly Lake, *Suksdorf 3509* (WS); north slope Mount St. Helens, *Gorman 5843* (WS); *Meyer 762* (WS); *St. John, et al. 7371* (WS). Snohomish County: Silverton, *Bonck 148* (WS). Whatcom County: Mount Herman, *Thompson 8049*; Mount Baker, *Turesson 22* (WS); Sourdough Mountain, *St. John 6836* (WS); Winchester Mountain, *St. John 8972*. Yakima County: Mount Aix, *Thompson 15023*; Mount Adams, *Henderson s.n.*; Suksdorf *3442*; *3516*; *4355*; *6850*; *August 14, 1898* (all WS); Bald Mountain ridge, *St. John 7788* (WS); Gold Hill, *Pickett 1364* (WS).

IDAHO. Kootenai County: Near Fernan Lake shore, Coeur d' Alene, *Rust s.n.* (WS).

MONTANA. Beaverhead County: Sheep Creek, near Wisdom, *Berghuis 23*. Flathead County: Camp Misery, Mount Aeneas, *Harvey 3325* (MONTU); Big Creek, *Edie 7* (MONTU); 2 miles southeast of Essex, *Brenckle* and *Shinners 41–093* (RM); top of Columbian Mountain, *Rogers* and *Rogers 1155* (WS); China Wall, *Kirkwood 2292* (MONTU); head of Moose Creek, China Wall, *Kirkwood 2330* (MONTU). Gallatin County: Bridger Mountains, 3 miles north of Brackett Creek, *Hitchcock* and *Muhlick 12446* (WS); Spanish Basin, *Rydberg* and *Bessey 4850* (RM). Glacier National Park: Sperry Glacier, *Umbach 826* (NY); Museum (Clements) Glacier, *Elrod s.n.* (MONTU); trail from Logan Pass to Hidden Lake, *Nelson* and *Nelson 3158* (RM); Clements-Reynolds saddle, Logan Pass, *Ewan 18474* (UC); Glacier Park, *Osterhout 8106* (RM). Lake County: 6 miles southeast and high above McDonald Lake, Mission Range, *Hitchcock 18327*. Lincoln County: Mount Mcdougal, Kootenai Mountains, *Umbach 139* (NY). Powell County: 6 miles south of Big Prairie Ranger Station, *Hitchcock 18815*.

BRITISH COLUMBIA. Vermilion Lakes, *Edith M. Farr 1013* (TYPE! deposited at NY); Lardo, Selkirk Mountains, *Shaw 695* (NY); Sage Pass, *T. M. C. Taylor 8611* (UBC); Antimony Mountain, Lytton, *Tisdale s.n.* (UBC); Cowiche Lake, Cottonwood Creek (Nanaimo District), *Simpson* and *Simpson s.n.* (WS); Lake House, Skagit River, *Macoun 76757* (WS); "probably near Lumby" (*sic*), *Anderson s.n.* (WS); Cameron River valley, Vancouver Island, *Rosendahl 1996* (UC).

ALBERTA. Upper Waterton Lake near Bungalow Camp, *Nelson* and *Nelson 4727* (RM); Upper Carthew Lake, Waterton Lakes National Park, *Hitchcock* and *Martin 7906*; Prince of Wales Hotel, Waterton, *Breitung 15897* (UC); Cameron Lake, Waterton Lakes National Park, *Ewan 18497* (UC); Waterton Lakes Park, *Moss 3352* (UC).

VOUCHERS FOR CHROMOSOME COUNTS OF P. LEPTOSEPALA RYDB. The vouchers for chromosome counts of this species as well as for others cited in this paper are deposited in the herbarium of the University of Washington, Seattle. All 18 collections were $n = 33$. WASHINGTON. Chelan County: *Kruckeberg 3319* (population sample of ten plants at Blewett Pass). Clallam County: Mount Angeles, *Kruckeberg 3809*. Jefferson County: Anderson Pass, Olympic National Park, *Kruckeberg 4010*. Kittitas County: Upper Teanaway River, *Kruckeberg s.n.*, July, 1951; Wenatchee Mountains, *Kruckeberg 2963, 3050, 3219, 3238, 3253, 3257, 3287, 3945, 3953, 3965, 3968*. Lewis County: Egg Butte, Goat Rocks Primitive Area, *C. Leo Hitchcock s.n.* Pierce County: Rainier National Park, *Kruckeberg 3805*. Skamania County: Mount St. Helens, *Kruckeberg 3978, 3993*. Snohomish County: Stillaguamish-Sauk rivers basin, *Kruckeberg 3245, 3246*; Twin Lakes above Monte Cristo, *Kruckeberg 3948*. Whatcom County: Mount Baker area, *Kruckeberg 3797, 3801, 3802*. Yakima County: Chinook Pass area, *Kruckeberg 3260, 3804*.

VOUCHERS FOR CHROMOSOME COUNTS OF OTHER TAXA

Phacelia corymbosa Jepson. ($n = 11, 22$). CALIFORNIA. Lake County: 4 miles northeast of Middletown, *Kruckeberg S–214* ($n = 22$). OREGON. Josephine County: Illinois River road, *Kruckeberg G–109* ($n = 22$).

Phacelia frigida Greene. ($n = 22, 23$). CALIFORNIA. Amador County: summit of Carson Spur, *Constance 3090* (UC) (tetraploid). El Dorado County: Meeks Bay, Lake Tahoe, *Rollins 3029* (UC) (tetraploid). Fresno County: Seldon Pass, *Kruckeberg 3491* ($n = 33$). Lassen County: slopes of Mount Lassen, *Kruckeberg 3710* ($n = 33$). Mono County: east slope of Mono Crater, *Constance* and *Bacigalupi 3435* (UC) (tetraploid); one-fourth mile east of Sonora Pass, *Constance* and *Bacigalupi 3437* (UC) (tetraploid). NEVADA. Washoe County: east side of Mount Rose Pass, *Constance* and *Mason 2797* (UC) ($n = 22$). OREGON. Douglas County: North Junction, Crater Lake National Park, *Kruckeberg 3781* ($n = 33$). Deschutes County: three miles south of Lava Lake, McKenzie Pass area, *Kruckeberg,* July 1950 ($n = 22$). Hood River County: Mount Hood, above Cloud Cap, *Kruckeberg 4000* ($n = 33$). Klamath County: northeast rim of Crater Lake near Palisade Point, *Constance 3362* (UC) (tetraploid).

Phacelia heterophylla Pursh. ($n = 11, 22$). OREGON. Jackson County: Neil Creek, *Kruckeberg G–116* ($n = 11$).

Phacelia leucophylla Torr. ($n = 22$). OREGON. Deschutes County: Between Tumalo and Sisters, *Kruckeberg 2071*. Jackson County: Blair quarry near Ashland, *Kruckeberg G–131*. Wallowa County: Upper Imnaha River above Coverdale Guard Station, *Kruckeberg G–229*. Wasco County: 3 miles east of junction of Madras-Mt.Hood and Maupin-Mt. Hood highways, *Hitchcock 19651*. WASHINGTON. Kittitas County: 2 miles below junction of Hurley Creek and Liberty-Beehive roads, *Kruckeberg 3240, 3254, 3255*; lower Teanaway River valley, *Kruckeberg* (*s.n.*), July 1951; Mt. Lilian, *Kruckeberg 3227*; Swauk Creek, *Kruckeberg 3317*. Klickitat County (var. *Suksdorfii* Macbride): White Salmon, *Phillips* (*s.n.*) September 1952; between Blockhouse and Klickitat, *Kruckeberg 3305*; between Bingen and Lyle, *Kruckeberg 3306*. Yakima County: Satus Pass, *Kruckeberg 3818*.

Phacelia mutabilis Greene. ($n = 11, 22$). CALIFORNIA. Sierra County: Between Webber and Meadow Lakes, *Constance, Bacigalupi* and *Nasir 3472* (tetraploid). OREGON. Deschutes County: 3 miles east of McKenzie Pass, *Constance 3456* (tetraploid). Jackson County: Rogue River Natural Bridge, 2 miles southwest of Union Creek, *Kruckeberg 2017* ($n = 22$). Wallowa County: Hat Point, *Kruckeberg 2470* ($n = 22$). Crater Lake National Park: along Rim Drive, 3 miles above Park headquarters, *Kruckeberg 3779* ($n = 22$).

Phacelia nemoralis Greene. ($n = 11, 22$). OREGON. Coos County: 2 miles east of Bridge, *Kruckeberg 3314* ($n = 22$). WASHINGTON. Aberdeen area, *Kruckeberg 3815, 3816, 3817*. Skamania County: Spirit Lake, *Kruckeberg 3814*; Washougal River, *Kruckeberg,* July 1953 (greenhouse plant from seed collected by *R. Ornduff* ($n = 22$).

ACKNOWLEDGMENTS. The author wishes to express his gratitude to two students of *Phacelia* at the University of California, Dr. Lincoln Constance and Dr. L. R. Heckard who, through many cooperative efforts and stimulating exchanges of ideas have materially aided this study. Thanks are also due to Mr. Paul Pascal of the University of Washington for the Latin translation, to the several curators of herbaria who made their collections available to the writer, and to my wife for assistance with the drawings.

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THE DISTRIBUTION OF QUERCUS BOYNTONI

CORNELIUS H. MULLER

Quercus boyntoni Beadle was discovered near the summit of Lookout Mountain in Etowah County, Alabama, in 1900. Beadle (1901) named the plant after its collector and the species was recognized subsequently by Small (1913, 1933) and by Trelease (1924). Sargent (1918) reduced it to the status of a variety of *Q. stellata* Wang., stating that "the dwarf habit of this little oak is due probably to the exposed position and high altitude where it grows."

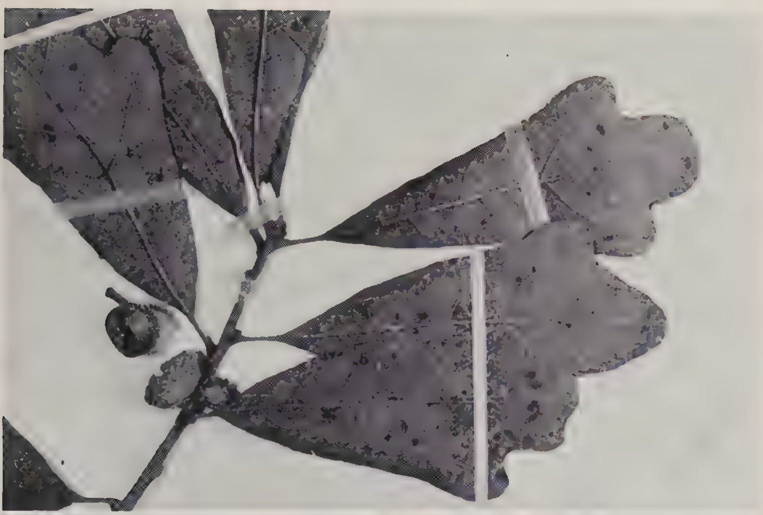
In 1942 there first came to my attention a series of specimens of a dwarf oak collected in 1934 in Angelina County, eastern Texas, by Effie Boon and by B. C. Tharp. The distinction between this and *Quercus stellata* was obvious, but the disposition of the Angelina County plant posed a problem, especially in the light of shrubby forms of other tree species known to occur in the prairie regions of Texas. Its segregation appeared unwise without a study of the plant in the field. Consequently, in my treatment of the oaks of Texas (1951) these specimens were included in *Q. stellata*. It is to this inclusion that the description of *Q. stellata* owes such characters as "small shrubs" and "leaves . . . obtriangular . . . bases cuneate . . . blades undulately . . . 2– to 4–lobed." The Boon collection cited from Angelina County under *Q. stellata* should have been identified as *Q. boyntoni.*

Recently I devoted an entire day in the field in Angelina County to a search for *Quercus boyntoni* and a study of its distribution compared with that of the related species. This was followed by a study of borrowed specimens of this species from the United States National Herbarium, including the Biltmore series and the Charles Mohr collection containing some Boynton specimens upon which Beadle based his original description. For this loan I am deeply indebted to the curator. All the Alabama specimens cited are deposited in the United States National Herbarium, while the Texas specimens cited are in my private herbarium. Duplicates of my own collections have been sent to the United States National Herbarium and otherwise distributed.

There follows an amplified description of *Quercus boyntoni* based upon both Alabama and Texas specimens. It should be emphasized that this description might as well have been drawn from one population as the other, so similar are the two.

QUERCUS BOYNTONI Beadle, Biltmore Bot. Studies 1:47. 1901. *Quercus stellata* var. *boyntonii* Sarg., Bot. Gaz. 65:437. 1918.

Rhizomatous shrubs 20 cm. to 3 m. tall (or 5 m., *fide* Beadle), trailing or sometimes semi-erect; twigs 1.5–3 mm. thick, densely fulvous-tomentulose with a mixture of simple appressed glandular hairs and moderately spreading stellate hairs, the pubescence darkening and persisting through the second season; buds 2–3 or even 4 mm. long, ovoid, acute or sometimes rounded, russet, sparsely pubescent; stipules deciduous, 3–5 mm. long, subulate, sparsely hairy; leaves deciduous or subevergreen, thin and rather soft, 5–10 (12) cm. long, 2–6 or rarely 8 cm. broad, cuneate to oblanceolate, obovate or oblong, characteristically roundly 3-lobed at the broad apex or sometimes 5-lobed above the entire cuneate base, margins minutely cartilaginous-revolute, upper surface glossy, in youth sparingly glandular-puberulent and with scattered stellate hairs, at length glabrate or the stellate pubescence persistent especially about the midrib, lower surface dull, persistently fulvous-glandular-puberulent and stellate-pubescent or the pubescence silvery, the veins about 6 to 8 on each side, very irregular and with some intermediates, those passing into the lateral lobes very prominent, slightly raised above and prominently so beneath, markedly and irregularly branching and anastomosing; petioles 5–10 mm. long, moderately slender, persistently pubescent like the twigs; staminate catkins 3–6 cm. long, fulvous-glandular-puberulent and stellate-pubescent, the puberulent anthers well-exserted from the ciliate perianth; pistillate catkins about 5 mm. long, about 3-flowered, and subsessile, densely fulvous-pubescent; fruit annual, solitary or paired on peduncles 2–10 or rarely even 35 mm. long; cups 10–13 mm. broad, 5–10 mm. high, deeply cup-shaped or more shallow, the scales densely fulvous- or silvery-tomentulose, the bases moderately or markedly thickened, the thin apices closely appressed, the acorns 10–17 mm. long, 7–10 mm. broad, broadly or narrowly ovoid, the ends broadly rounded, brown and minutely puberulent especially about the apex, about one-half or only one-third included.



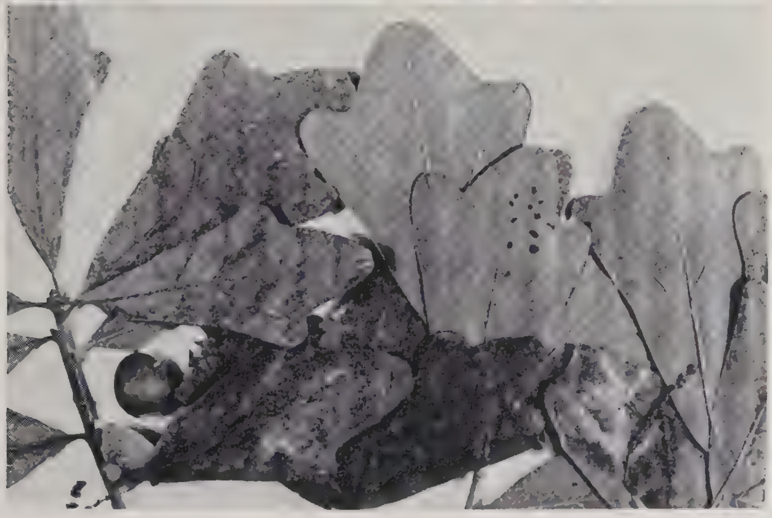


FIG. 1 (top). *Quercus boyntoni* Beadle, the lectotype specimen from Etowah County, Alabama, *C. L. Boynton s. n.*, sheet no. 780302, US. FIG. 2 (bottom). *Quercus boyntoni* Beadle, a typical specimen from Angelina County, Texas, *C. H. Muller 9609*.

Specimens examined. ALABAMA: Etowah County, about summit of Lookout Mountain, near Gadsden, May 1900, *C. L. Boynton s.n.* (Herb. Chas. Mohr); July 29, 1900, *C. L. Pollard* and *W. R. Mazon 339*; September 1, 1900, *Boynton s.n.* (lectotype); April 1901, *T. G. Harbison s.n.*; April 26, 1901, *collector unknown 1905* (Biltmore Herb.); October 12, 1901, *collector unknown 1905a* (Biltmore Herb.); September 25, 1902, *collector unknown 1905c* (Biltmore Herb.). Jefferson County, glades along Lost Creek, Shades Mountain, near Birmingham, April 18, 1931, *E. J. Palmer 38946*. TEXAS: Angelina County,[1] "Charlie Massengill's Farm," August 15, 1934, *E. Boon 473*; August 16, 1934, *Boon 492*; September 16, 1934, *Boon s.n.*; Shawnee Switch, September 16, 1934, *B. C. Tharp s.n.*; 1 mi. W. of Shawnee Creek, 2 mi. E. of Shawnee Store, Shawnee Prairie, 9.5 mi. S.W. of Huntington, August 26, 1953, *C. H. Muller 9609, 9610, 9611*.

The Alabama collections taken in the first years of the century are singularly lacking in certain data. The Biltmore specimens, of course, do not bear the collectors' names. "Black Creek near Gadsden" is mentioned on a Charles Mohr label with a plant apparently collected by Boynton and appearing on the same sheet with another Boynton collection. Another Mohr sheet bears the only reference to habit—"trailing shrub not over 2 feet high"—written in pencil on a crude label and accompanying a duplicate of Boynton's collection of May 1900. These Mohr herbarium specimens seem to be the only examples of Boynton's collections extant. One of them (US no. 780303) bears the notation "Biltm. herb." Another (US no. 780302) is here chosen as the type on the grounds that it is the only mature specimen of Boynton material available and was seen by Beadle prior to the publication of the species. Beadle refers to Boynton collections in April and October of 1900, but only May and September collections appear. The Biltmore herbarium contains no Boynton material at all.

Small (l. c.) describes the range of *Quercus boyntoni* as extending along ridges in the Alleghany Valley into Georgia. I have not seen any specimens of this species from Georgia, but its occurrence there would be expected.

The yellow pubescence on the lower leaf surface, referred to by Sargent, may be due to the age of the dried specimens. The 1934 collections from Texas match those of Alabama taken in 1900 and 1901. The 1953 Texas collections have (at the date of writing) a more silvery pubescence that may yellow with age.

That *Quercus boyntoni* and *Q. stellata* are closely related is clearly indicated by the similarity of the fruit, puberulence of anthers, and the dense almost mealy puberulum or tomentulum of the twigs. That they deserve specific distinction, however, is equally plain. The shrubby habit of *Q. boyntoni* is not in any way related to the growing conditions. Neither the elevation of the Lookout Mountain site (300 m., *fide* Beadle) nor Sargent's reference to "in the shelter of narrow glades" indicates the degree of altitude and exposure that constitutes a rigorous habitat. A normally erect tree species such as *Q. stellata* (however small of stature in its xeric western range) is not changed by such moderate rigor to a sprawling rhizomatous shrub as little as 20 cm. tall at maturity. The even lesser stature of the lowland Texas population of *Q. boyntoni,* growing at about 60 m. elevation, further emphasizes the genetic nature of this character. The leaf shape and thin texture of the blades of *Q. boyntoni* are constant characters in which it differs further from *Q. stellata.*

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[1] The occurrence in Angelina County, Texas, of a community named Boynton located a few miles from the Shawnee localities is purely coincidental and in no way related to the name of the species, which was derived from that of its first collector in Alabama.

Although most of the collectors' references to site conditions in the Alabama populations have stressed "shallow soil," the Texas plant occurs on a deep sandy soil in the valley of a creek. The species was found by Boon and Tharp out on Shawnee prairie and in other prairie locations, but I failed to find it except in the shelter of forest.

In the Texas population *Q. boyntoni* occurs under *Pinus taeda* and *Liquidambar styraciflua* mixed with arboreal *Q. drummondii* Liebm. Although there is some little evidence of hybridization of *Q. boyntoni* with *Q. drummondii* (*Muller 9605, 9607*), the shrub species occurs abundantly in pure form associated with the tree species equally free of hybridity. Furthermore, saplings of the tree species were noted as erect plants, showing neither the trailing habit nor the leaf characters of *Q. boyntoni* (*Muller 9606*). The surrounding clay and gravel hills are abundantly populated by typical *Q. stellata* which is not found on deep sand (*Muller 9604*).

An inconspicuous dark green shrub trailing down banks and mixed with shrubs of taller stature is easily overlooked, especially if its fruit is hidden by the leaves and its leaf form is sufficiently similar to surrounding trees to cause it to be taken for a seedling of these. It is therefore unlikely that the full distribution of *Quercus boyntoni* is indicated by the available herbarium specimens. In fact, Mrs. Boon indicated (manuscript map in personal communication) four localities in Angelina County in which she had encountered *Q. boyntoni,* one in the Shawnee Creek drainage and the other three in the Biloxi (Balaxy) Creek drainage. One locality in each drainage is authenticated by specimens here cited. Between Texas and eastern Alabama there very possibly exists a number of sandy creek valleys similar to that of Shawnee Creek in which *Q. boyntoni* may be found.

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ON THE GENERIC LIMITS OF ERIOPHYLLUM (COMPOSITAE) AND RELATED GENERA

Sherwin Carlquist

While recent authors largely agree in definitions of species referable to the genus *Eriophyllum* (Compositae, tribe Helenieae) or its neighboring genera, the generic disposition of these synonymy-laden species has been less satisfactory. The genera studied here correspond to those grouped by Rydberg (1915) in the subtribe Eriophyllanae. Since species of all of these genera have been subject to repeated reassortment, all of the taxa required examination before any resolution could be attempted.

The high degree of disagreement seems to stem from the small number of characters by which these genera may be recognized. In the instance of these, and many other highly reduced members of the Compositae, it may well be that relationships will never be properly understood, owing to the fact that only a limited number of characters has been left by evolution for the taxonomist to use. These characters have been taxed to the utmost by the systematist, and decisions have necessarily been arbitrary to a large extent. For this reason, the addition of a cytological character, chromosome number, and a review of morphological characters, particularly in the anatomical details which underlie them, seemed highly desirable.

Historical Survey

A glance at the historical record will show that this subtribe is a particularly poorly understood one. The genus *Eriophyllum,* created by Lagasca for a perennial species, *E. staechadifolium,* was adopted by Gray (1884) to include all the perennial species, though he first referred these species to *Bahia* (1876). Subsequent authors have placed all perennial species in *Eriophyllum.* The chief problem, then, was whether or not to refer annuals similar in aspect to the same generic concept. The genus *Actinolepis* had been set up by de Candolle to receive annuals possessing pappus (including species of *Baeria*), while he had erected the genus *Monolopia* for the epappose species. From the time of Gray on, however, persuasive similarities in aspect of some of the annuals to some of the perennials led to their inclusion in *Eriophyllum,* rather than *Actinolepis* or *Monolopia,* with the result of converting *Eriophyllum* into a capriciously heterogeneous assemblage poorly differentiated from incoherent groups of annual species left as outliers. Typical of the attitudes involved in this segregation is the description by Greene (1897) of *Eriophyllum* (now a *Pseudobahia*) *Heermannii* as "wholly an *Eriophyllum,* not only as to habit, but as to the character of the involucre and achenes," while two species of *Eriophyllum* later, he finds *E. ambiguum* (considered here as close to the perennials) "A plant with more the habit of a *Monolopia* than any of the foregoing."

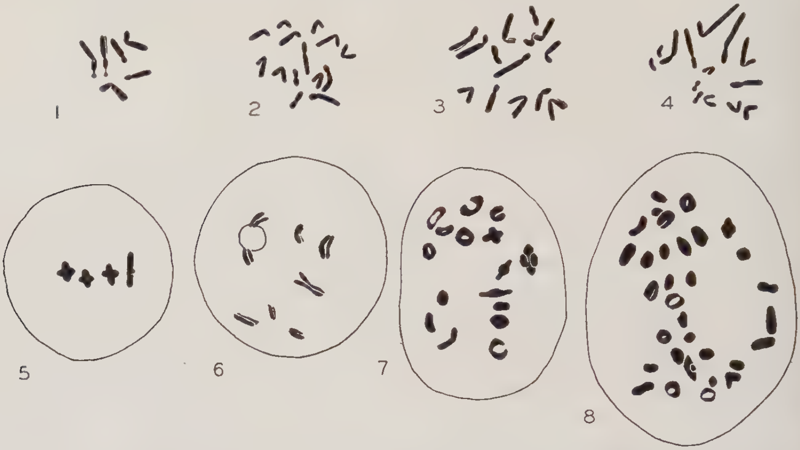
ERIOPHYLLUM. Gray (1884) added the species *ambiguum* to the perennials forming *Eriophyllum,* denoting all of these as "section *Trichophyllum.*" Once this species had been allowed in *Eriophyllum,* however, logic demanded the admission of others, and he appended a "section *Actinolepis*" consisting of the entities *Eriophyllum nubigenum, E. multicaule, E. Pringlei, E. lanosum,* and *E. Wallacei.* Greene (1897) restored *Actinolepis* as a genus, but to the perennials of *Eriophyllum* he added *E. bahiaefolium* and *E. Heermannii,* formerly considered by Gray under *Monolopia.* Rydberg (1915) subtracted these last two species, but added *Eriophyllum nubigenum* (formerly in *Actinolepis*), *E. Congdonii,* a recently named species close to both *E. ambiguum* and *E. nubigenum,* and *E. minus.* This last species, known only from the type specimen, was formerly treated as *Monolopia minor,* though it is actually a *Baeria* (see below). Jepson (1925) restored the full complement of species used by Gray, without sectional distinctions, adding, however, *Eriophyllum Heermannii,* and a species for which Johnston (1923) created the monotypic genus *Eremonanus, E. mohavense.* Constance (1937) treated the genus similarly to Jepson, removing *Eriophyllum Heermanii* to *Monolopia* and recognizing *Eremonanus mohavense.*

ACTINOLEPIS. While Gray treated this group of pappose annuals as a genus in 1876, he considered it a section of *Eriophyllum* in 1884. Greene, reviving it as a genus, included *A. nubigena,* like Gray, though this species is close to *Eriophyllum ambiguum,* which both regarded as an *Eriophyllum.* Greene's *Actinolepis* agrees with Gray's. Rydberg performed a maximum of segregation among the annuals, leaving the contents of Gray's *Actinolepis* not included in *Eriophyllum* to be distributed among *Actinolepis* and a new genus, *Antheropeas.*

Actinolepis contained only *A. multicaulis* and *A. Pringlei,* while *Antheropeas* was created for a close pair of species, *A. lanosum* and *A. Wallacei.* Dubious of the segregation of numerous small genera, Jepson (1925) and Constance (1937) restored all the *Actinolepis* and *Antheropeas* species to *Eriophyllum* without sectional distinctions.

MONOLOPIA; PSEUDOBAHIA. Gray, subsequent to his original treatment of *Monolopia* (1876) soon recognized (1884) that the contents of this epappose genus could be split into two sections. The tall, virgate species with subentire leaves, *M. major* and *M. gracilens,* became "section *Monolopia,*" while the low, Eriophyllum-like plants with pinnatifid leaves, *M. bahiaefolium* and *M. Heermannii,* were "section *Pseudo-Bahia.*" Influenced by the Eriophyllum-like qualities of the latter, Greene placed them in *Eriophyllum,* while Rydberg created a new genus, *Pseudobahia,* for them; both authors retained the remaining species in *Monolopia.* Jepson's treatment agrees with Greene's except for placing *Eriophyllum bahiaefolium* of Greene in *Monolopia* (without sections). Constance, though not dealing with this group directly, accepted Gray's treatment provisionally. It remained for Crum (1940) to offer a careful and detailed revision of

Monolopia (excluding *Pseudobahia*). The writer follows her treatment. Crum suggested that *Monolopia minor,* a species the type and only collection of which had apparently been seen by none of the authors mentioned, was actually a *Baeria.* Evidence accumulated by Mrs. Roxana S. Ferris confirms Miss Crum's opinion and in a recent paper (Ferris, 1955) she has made the necessary nomenclatural changes.



Figs. 1–4. Metaphase of somatic divisions in root tips. 1, *Pseudobahia Heermannii, Carlquist 302*; 2, *Eriophyllum multicaule, Carlquist 293*; 3, *Eriophyllum ambiguum, Carlquist 312*; 4, *Eriophyllum lanatum* var. *arachnoideum, Carlquist 336.* Figs. 5–8. Meiotic divisions of pollen mother cells. 5, first metaphase, *Pseudobahia bahiaefolia, Bacigalupi & Carlquist 4014*; 6, diakinesis, *Eriophyllum confertiflorum, Carlquist 330*; 7, first metaphase, *Eriophyllum confertiflorum, Carlquist 325*; 8, first metaphase, *Eriophyllum confertiflorum* var. *tanacetiflorum, Carlquist 327.* All × 1200.

Syntrichopappus. The distinctive pappus of *S. Fremontii* prevented it from being confused with any of the other annuals, though Gray, who named it, realized it was closely related to them. Soon effacing his error of placing a new species, *S. Lemmonii* (thought epappose until now) in *Actinolepis,* Gray (1884), with remarkable intuition, designated it as the second species of *Syntrichopappus.* All subsequent authors have accepted this treatment.

The writer's disposition of these taxa is seen in the table of chromosome numbers, with the exception of *Eriophyllum mohavense,* which he regards as coordinate with *E. Pringlei,* and *E. nubigenum,* which is to be placed beside *E. ambiguum* and *E. Congdonii.*

Methods

To obtain chromosome numbers, young heads, or root tips of plants grown from seed, were fixed in a Carnoy's solution (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). To assure quick penetration, it was necessary to break open the heads before placing them in the fluid, or aspirate them with a vacuum pump directly after immersion. The usual acetocarmine squash technique was employed for both pollen mother cells and root-tips. The designation "2n" indicates that the number was derived from a somatic division, while "n" denotes a count made from meiotic material. Voucher specimens were made at the same time buds were fixed, or, if plants grown from seed were used, specimens of these were prepared. A set of these specimens has been deposited in the Herbarium of the University of California at Berkeley, and replicates of most of these have been distributed to other herbaria.

Anatomical information was derived from both cleared and sectioned material. Mature flowers from the writer's collections preserved in Carnoy's fluid or from numerous herbarium specimens were cleared in 2.5 per cent aqueous NaOH, dehydrated, and stained in safranin. Heads of plants in the writer's collections fixed in Carnoy's fluid were also dehydrated by means of Johansen's tertiary butyl alcohol series, embedded in paraffin, sectioned, and stained with a safranin-fast green combination.

The writer wishes to express especial appreciation to Dr. Lincoln Constance, at whose suggestion the problem was undertaken, for valuable comment and advice. Thanks are due to him and to Dr. Herbert L. Mason, Dr. G. Ledyard Stebbins, Jr., and Miss Annetta Carter for reading the manuscript and offering suggestions. Acknowledgment is also extended to those who provided fixed material and specimens, and whose names appear among the collections listed in Table 1.

Cytology

The accompanying table shows that distinctive chromosome numbers characterize the various taxa. *Eriophyllum* sect. *Eriophyllum* contains diploids having n = 8 as well as polyploid derivatives. While no diploids were found in *E. Jepsonii, E. latilobum, E. Nevinii,* or *E. staechadifolium,* both *E. confertiflorum* and *E. lanatum* contain diploids and tetraploids (figs. 4, 6, 7). No correlation was found in the relative size of parts of diploid versus polyploid plants. In fact, the polyploids showed more diminutive parts in most instances. Pollen-size differences likewise were negligible. A strong exception is the extremely robust octoploid *E. confertiflorum* var. *tanacetiflorum* (fig. 8).

The meagre coverage of the large *E. lanatum* complex suggests that both diploids and tetraploids may be found independently in at least two of the varieties. Since a better coverage of this group did not seem necessary for the purposes of generic definition, the nature and distribution of diploid and polyploid plants presents an interesting subject for further investigation. Likewise, the relative frequence of diploids and polyploids in *E. confertiflorum* remains to be studied.

The annuals of *Eriophyllum,* considered here as a section, *Actinolepis,* are characterized by a haploid chromosome number of 7 (figs. 2, 3). The

TABLE 1. CHROMOSOME NUMBERS

SPECIES	COLLECTION	APPROXIMATE LOCALITY	NUMBER
Eriophyllum Lagasca section *Eriophyllum*, sect. nov. (perennials)			
E. confertiflorum (DC.) Gray	*Carlquist 330*	Fort Tejon, Kern County*	n = 8
	Carlquist 338	Pasadena, Los Angeles County	n = 8
	Carlquist 316	Avalon, Los Angeles County	n = 16
	Carlquist 318	Arroyo del Puerto, Stanislaus County	n = 16
	Carlquist 325	Coulterville, Mariposa County	n = 16
	Carlquist 334	Midpines, Mariposa County	n = 16
E. confertiflorum (DC.) Gray var. *tanacetiflorum* (Greene) Jepson	*Carlquist 327*	Coulterville, Mariposa County	n = 32
E. Jepsonii Greene	*Carlquist 317*	Arroyo del Puerto, Stanislaus County	n = 16
E. lanatum (Pursh) Forbes var. *achillaeoides* (DC.) Jepson	*Chisaki 565*	Black Oak Villa, Lake County	n = 8
	Post 105	Alder Point, Mendocino County	n = 8
	Balls & Everett 11 October 1952	Lava Beds, Modoc County	2n = 32
	Gillett 266	Lassen National Park, Shasta County	n = 16
	Sweeney 8 May 1953	Black Oak Villa, Lake County	n = 16
E. lanatum (Pursh) Forbes var. *arachnoideum* (F. & L.) Jepson	*Carlquist 336*	Little River, Mendocino County	2n = 16
E. lanatum (Pursh) Forbes var. *grandiflorum* (Gray) Jepson	*Carlquist 324*	Coulterville, Mariposa County	n = 8
	Heckard & Sweeney 341a	Oroville, Butte County	n = 16
E. latilobum Rydberg	*Carlquist 305*	San Mateo, San Mateo County	n = 16
E. Nevinii Gray	*Carlquist 315*	Avalon, Los Angeles County	n = 16
E. staechadifolium Lagasca	*Carlquist 307*	Castroville, Monterey County	n = 16
	Carlquist 309	Piedras Blancas, San Luis Obispo County	n = 16
	Carlquist 335	Asilomar, Monterey County	n = 16

TABLE 1. CHROMOSOME NUMBERS (continued)

Eriophyllum Lagasca section *Actinolepis* Gray (annuals)			
E. ambiguum Gray	*Carlquist 312*	Hobo Hot Springs, Kern County	$n = 7$ $2n = 14$
	Carlquist 313	Red Rock Canyon, Kern County	$n = 7$
	Carlquist 329	Fort Tejon, Kern County	$n = 7$
	Gillett 411	Edison, Kern County	$n = 7$
	Gillett 417	Mt. Breckenridge, Kern County	$n = 7$
E. Congdonii Brandegee	*Carlquist 333*	El Portal, Mariposa County	$n = 7$
E. multicaule Gray	*Bacigalupi 4117*	Gonzales, San Benito County	$n = 7$
	Carlquist 293	Oceano, San Luis Obispo County	$n = 7$
E. Pringlei Gray	*Carlquist 296*	Boron, Kern County	$n = 7$
Antheropeas Rydberg			
A. lanosum (Gray) Rydberg	*Carlquist 337*	Las Vegas, Clark County, Nevada	$n = 4$
A. Wallacei (Gray) Rydberg	*Carlquist 295*	Boron, Kern County	$n = 5$
Monolopia DC.			
M. gracilens Gray	*Carlquist 306*	Hecker Pass, Santa Cruz County	$n = 12$
M. lanceolata Nutt.	*Carlquist 289*	Lost Hills, Kern County	$n = 10$
M. major DC.	*Carlquist 285*	Tracy, San Joaquin County	$n = 12$
M. stricta Crum	*Carlquist 288*	Lost Hills, Kern County	$n = 10$
Pseudobahia Rydberg			
P. bahiaefolia (Benth.) Rydberg	*Bacigalupi & Carlquist 4014*	North of Friant, Madera County	$n = 4$ $n = 3$
P. Heermannii (Dur.) Rydberg	*Carlquist 302*	Coulterville, Mariposa County	$2n = 6$
	Carlquist 304	Bagby, Mariposa County	$n = 3$
P. Peirsonii Munz	*Carlquist 287*	Ducor, Kern County	$n = 8$
Syntrichopappus Gray			
S. Fremontii Gray	*Carlquist 301*	Stoddard's Well, Kern County	$n = 6$
S. Lemmonii Gray	*Carlquist 314*	Cajon Pass, San Bernardino County	$n = 7$

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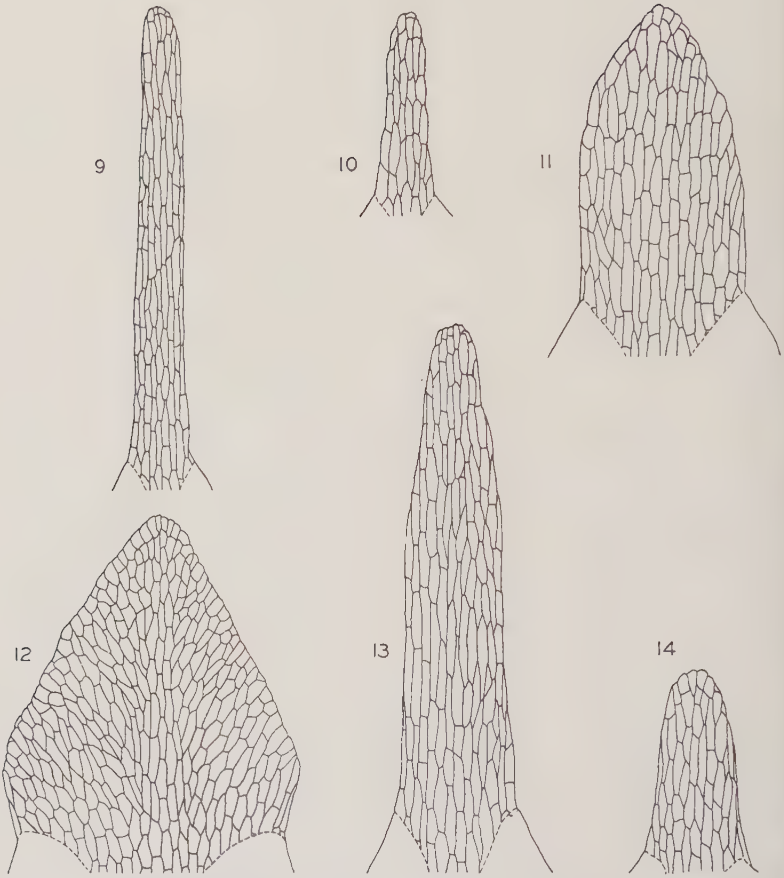
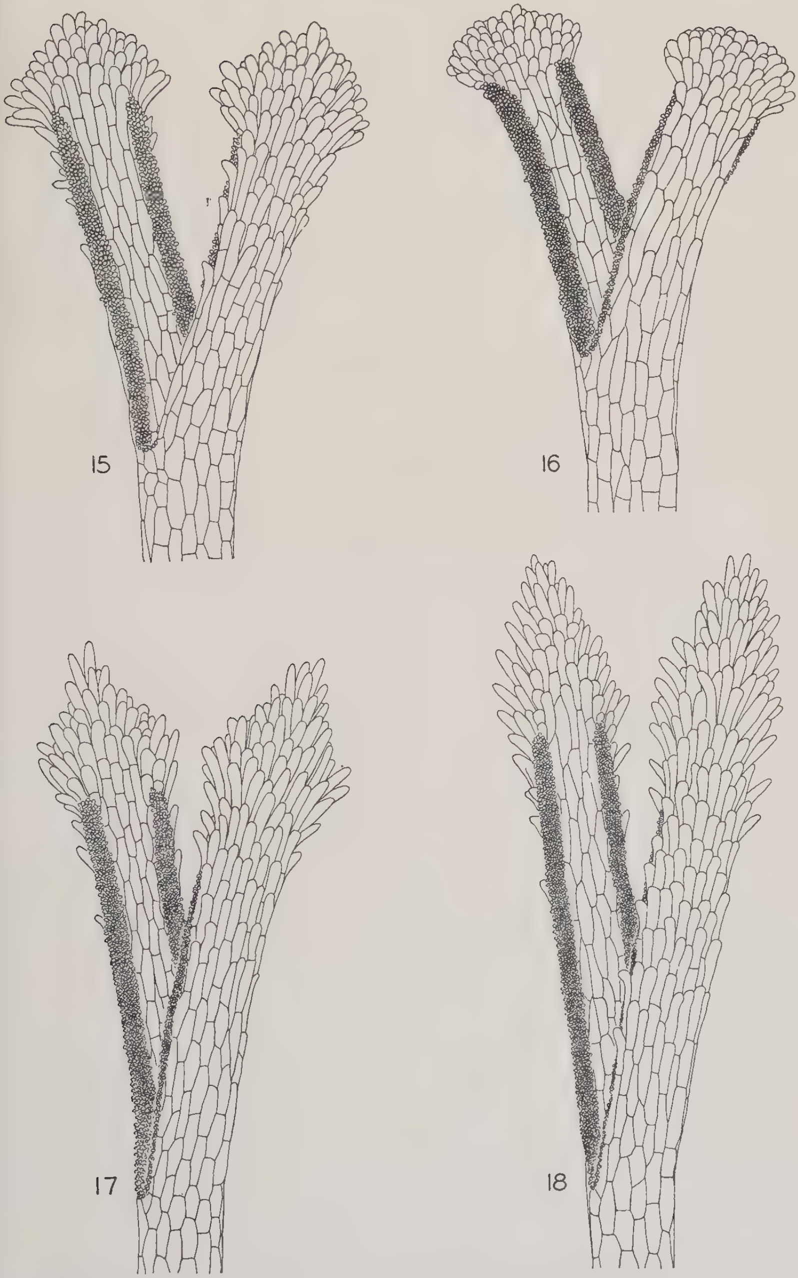
* Unless otherwise noted, all localities are in California.



Figs. 9–14. Stamen tips. 9, *Antheropeas lanosum, Carlquist 337*; 10, *Antheropeas Wallacei, Carlquist 295*; 11, *Eriophyllum Pringlei, Carlquist 296*; 12, *Pseudobahia Heermannii, Carlquist 304*; 13, *Syntrichopappus Fremontii, Carlquist 301*; 14, *Syntrichopappus Lemmonii, Carlquist 314*. All × 90.

two species of *Antheropeas* show numbers of 5 and 4 respectively. Though similar in habit to the seven-paired *Eriophyllum ambiguum,* both *Pseudobahia bahiaefolia* and *P. Heermannii* have the distinctive numbers $n = 4$ and $n = 3$ respectively (figs. 1, 5). *Pseudobahia Peirsonii,* a robust weedy plant, is seen to have $n = 8$, which may be tetraploid in relation to the $n = 4$ of this genus. The species of *Monolopia,* similar to *Pseudobahia Peirsonii* in habit, may also be polyploid, since their high chromosome numbers of ten and twelve suggest a derivative rather than a basic set. Further evidence would be needed to affirm this suggestion. The two species of the well-differentiated genus *Syntrichopappus* show $n = 7$ and $n = 6$ respectively.



FIGS. 15–18. Upper portions of styles. 15, *Eriophyllum staechadifolium, Carlquist 309*; 16, *Eriophyllum multicaule, Carlquist 293*; 17, *Antheropeas Wallacei, Carlquist 295*; 18, *Syntrichopappus Fremontii, Carlquist 301*. All × 85.

MORPHOLOGICAL AND ANATOMICAL CHARACTERS

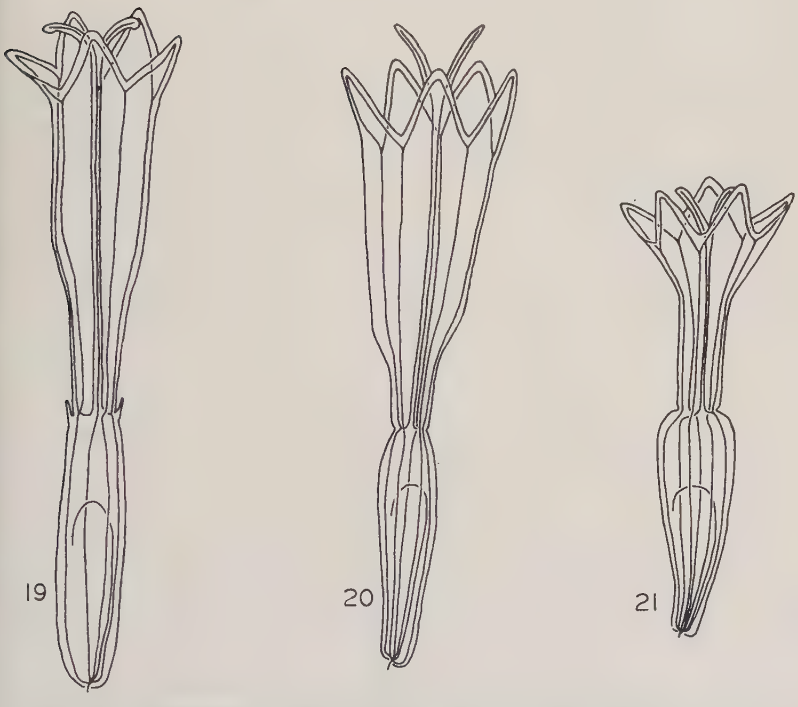
STAMEN TIPS. The terminal projection of the anther connective takes markedly different forms in the taxa considered here. The deltoid shape, widened above the base (fig. 12) is characteristic of many Helenieae, and is found throughout *Eriophyllum* sect. *Eriophyllum, Pseudobahia,* and *Monolopia.* Occasional specimens of *Eriophyllum* sect. *Eriophyllum* may exhibit deltoid tips tapered from the base. In *Eriophyllum* sect. *Actinolepis,* however, deltoid tips widened above the base may be found only in *E. ambiguum, E. Congdonii,* and *E. nubigenum.* In these three species, tips tapered from the base may also be found. In the remaining species of sect. *Actinolepis, E. multicaule, E. Pringlei,* and *E. mohavense,* tips tapered from the base are characteristic (fig. 11). These tips are relatively narrow and cuneate in some specimens of *E. multicaule.*

Antheropeas, on the contrary, shows conspicuously narrower subulate tips (figs. 9, 10), extremely long in *A. lanosum.* In a similar way, the species of *Syntrichopappus* exhibit quite attenuate stamen tips, varying from cuneate in *S. Lemmonii* (fig. 14) to lanceolate in *S. Fremontii* (fig. 13).

STYLE TIPS. The tips of the style-halves, frequently termed "style appendages," have long been recognized of diagnostic value. The predominant shape in the Helenieae is deltoid, tapering abruptly above a fringe of elongate hairs (fig. 15). Within both sections of *Eriophyllum* this shape is found to be characteristic, though some species show a very much blunted form. *E. multicaule* has nearly flattened tips (fig. 16), and is the most extreme expression of a blunted tip. *Pseudobahia* and *Monolopia* are found to have a deltoid tip such as shown in fig. 15. *Antheropeas,* on the other hand, has an appreciably more elongate tip, varying from narrowly deltoid to cuneate. Many style-tips of *A. lanosum* and *A. Wallacei* are much more attenuate than the one shown in fig. 17. In addition, in both species of *Antheropeas,* prominent elongate hairs terminate the style tips. The genus *Syntrichopappus* shows the most striking difference from the type found in *Eriophyllum,* the style tips being very much prolonged into a lanceolate form (fig. 18).

FLORAL VENATION. Though the floral vasculation of composites is highly stereotyped, certain differences may be found. The disk flowers alone serve for comparison here, since in the taxa studied, wide variation within a single population occurs in ray-flower venation. In the ray corolla, a series of veins runs the length of the corolla, forming interconnections at the tip. While characteristic patterns may be found, these are profoundly altered in depauperate or extremely robust plants. Some species, however, such as *Eriophyllum multicaule, E. nubigenum, E. Nevinii, Antheropeas lanosum* and *A. Wallacei,* show few if any interconnections between the veins at the tip of the ray.

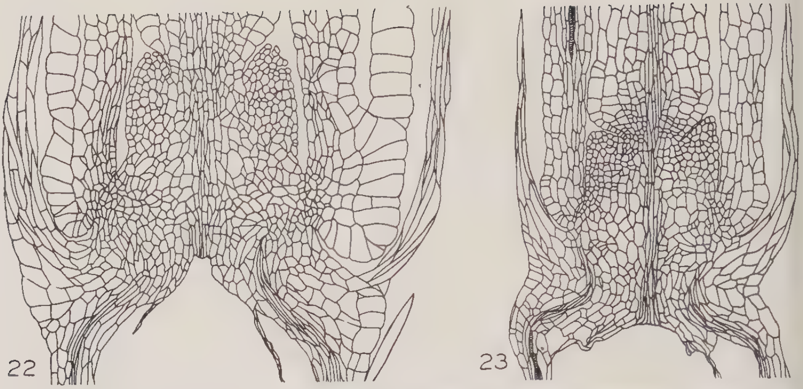
Disk flowers in the genera studied show an identical venation in the corolla, and either four, five, or six veins in the achene (figs. 19–21). An



Figs. 19–21. Disk flowers, showing venation. 19, *Eriophyllum lanatum* var. *grandiflorum, Carlquist 324*; 20, *Syntrichopappus Lemmonii, Carlquist 314*; 21, *Eriophyllum mohavense, Jepsen 17180a.* All × 14.

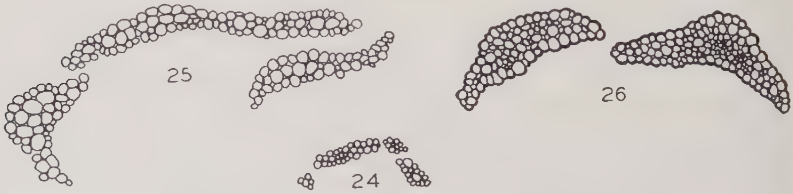
ovule trace and two style traces are always present; stamen traces, slightly better developed in the perennials of *Eriophyllum,* are usually rudimentary or absent. The species of *Eriophyllum* sect. *Eriophyllum* are characterized by four, sometimes five, achene-wall bundles (fig. 19), as are the members of the genus *Pseudobahia. Monolopia* and *Antheropeas* have four achene-wall bundles, while *Syntrichopappus* has five (fig. 20). In *Eriophyllum* sect. *Actinolepis, E. ambiguum, E. Congdonii, E. nubigenum,* and *E. multicaule* have four achene-wall bundles, while *E. Pringlei* and *mohavense* have five; occasionally six bundles appear in achenes of *E. mohavense* (fig. 21). The patterns of bundle interconnections are always the same in flowers having four, five, or six achene bundles respectively as shown (figs 19–21).

Pappus. Particular interest was focussed on finding if any constant characters besides annual versus perennial habit and 7 versus 8 (16, 32) chromosomes distinguish the annuals, sect. *Actinolepis,* of *Eriophyllum,* from the perennials, sect. *Eriophyllum.* Though differences largely of degree rather than of character may be found, such as the generally more indurate involucral bracts of the perennials, pappus structure offers a



FIGS. 22–23. Portions of longitudinal sections of achenes, showing pappus and basal portions of style and corolla in section; 22, *Eriophyllum Jepsonii, Carlquist 317,* palea at left seen in median section; 23, *Eriophyllum ambiguum, Carlquist 313.* Both × 80.

more nearly discrete distinction. In longitudinal section, the pappus base is wider in the perennials (fig. 22), the outer epidermis of the pappus forming a nearly continuous line with that of the achene wall. In the annuals, the achene top is more constricted at the pappus base (fig. 23). This is probably associated with the tendency of the pappus to reflex more widely at maturity in the annuals. Difference may also be seen in the structure of pappus as seen in transection. The paleae of the pappus of annuals vary from simple (fig. 24) to moderately thick (fig. 25), the extremes being represented in these two figures. While pappus paleae such as shown in fig. 25 may also occur in the perennials, paleae with more numerous layers of cells, some of the internal cells smaller, can be found only in the perennial species (fig. 26).



FIGS. 24–26. Transections of pappus paleae. 24, *Eriophyllum multicaule, Carlquist 293*; 25, *Eriophyllum Congdonii, Carlquist 333*; 26, *Eriophyllum Jepsonii, Carlquist 317*. All × 100.

The traditional differences in external structure of pappus are quite useful in differentiating the smaller genera. While at least a short crown of pappus or pappus-vestige is present in *Eriophyllum,* the genera *Monolopia* and *Pseudobahia* lack any such structure. *Syntrichopappus,* as the name implies, is characterized by a circle of numerous setae united at the

TABLE 2. COMPARISON OF ERIOPHYLLUM AND CLOSELY RELATED GENERA

	Eriophyllum section *Eriophyllum*	*Eriophyllum* section *Actinolepis*	*Antheropeas*	*Monolopia*	*Pseudobahia*	*Syntrichopappus*
Habit	perennial	annual	annual	annual	annual	annual
Leaves	pinnatifid to nearly entire	lobed (entire in a few plants)	entire to toothed	entire to toothed	pinnatifid, bipinnatifid	lobed or entire
Chromosome no.	n = 8, 16, 32	n = 7	n = 5, 4	n = 12, 10	n = 4, 3, 8	n = 7, 6
Stamen tips	deltoid, widened above base	deltoid, widened above or tapering from base	subulate	deltoid, widened above base	deltoid, widened above base	cuneate to lanceolate
Style tips	deltoid to blunt	deltoid to blunt	cuneate	deltoid	deltoid	lanceolate
Bundles in disk achene	4, 5	4, 5, 6 (depending on species)	4	4	4, 5	5
Pappus	short paleae	short paleae to a crown	paleae	entirely absent	entirely absent	ring of many setae or absent
Corolla hairs	glandular, scattered along tube and throat	glandular, scattered along tube and throat	glandular, scattered along tube and throat	glandular, scattered, plus non-glandular hairs at lobe-tips	glandular, grouped in a ring at base of throat	glandular, scattered along tube and throat

base. While all authors have considered *S. Lemmonii* epappose, populations of this plant contain a few individuals bearing the pappus typical of *S. Fremontii,* though the bristles are shorter and less numerous than in *S. Fremontii.* Despite the prolongation of four or five of the pappus paleae of *Antheropeas lanosum* into setae, there is no fundamental difference between the genus *Antheropeas* and the annuals of *Eriophyllum* in pappus structure.

Discussion

The various features already discussed as well as some additional points are summarized in Table 2. It will be seen that in addition to the chromosome number, other differences may be found to support the division of genera which is proposed here. Though the chromosomes of *Eriophyllum mohavense* and *E. nubigenum* have not been seen, other features of these rarities, which may now be extinct, make certain their placement in *Eriophyllum* sect. *Actinolepis. Eriophyllum nubigenum* appears to be an alpine extreme closely connected with *E. ambiguum* and *E. Congdonii. Eriophyllum mohavense,* despite its distinctive heads consisting of four (or three) flowers grouped around a short central projection of the receptable, is closely related to *E. Pringlei.* These two species agree in their discoid heads, the numerous short pappus paleae, the short, broadly funnelform corolla, morphology of stamen and style tips, etc. The writer does not agree with Johnston (1923) that *Eriophyllum* (*Eremonanus*) *mohavense* must be considered in conjunction with the monotypic genus *Dimeresia* Gray. *Dimeresia* seems only superficially similar by virtue of its two-flowered heads, while the larger flowers (larger than any of the above, with the exception of a few perennials of *Eriophyllum*), the prominent setose pappus, curiously involute at the base, the essentially opposite leaves, lacking any indications of lobes or teeth, all seem to remove it from consideration with any of the Eriophyllanae, including *Syntrichopappus.* Although Gray originally placed *Dimeresia* in the Inuleae, the treatment of Cronquist (1955), who includes this genus in the Senecioneae, seems the most acceptable.

The annuals of *Eriophyllum,* despite their differences from the perennials in chromosome number, are structurally close to them in such species as *E. Congdonii,* so that it has not seemed feasible to segregate the diverse contents of this group into still another genus. Consequently, recognition of them as a section of *Eriophyllum* seems most logical. *Antheropeas,* however, which is often accepted as part of *Eriophyllum,* seems to merit separation from the annuals by virtue of its lower chromosome numbers and notably different stamen-apex and style-tip structures. Likewise, the anomalous chromosome numbers of *Pseudobahia* reinforce the lack of pappus and aggregation of corolla hairs in distinguishing it from *Eriophyllum.* Chromosome numbers, habit, leaf characters, and corolla hairs in turn separate *Pseudobahia* from *Monolopia.*

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NEW SPECIES OF ELATINE IN CALIFORNIA

HERBERT L. MASON

In preparing the treatment of the Elatinaceae for a work on the flora of the marshes and ponds of California, it became clear that *Elatine* presents a perplexing problem in speciation. The differences between aquatic and terrestrial forms of the same species often seem greater than the differences between species. The genus is in need of a thorough cultural study designed to test the nature of characters and their validity as criteria of species. In the meantime one is faced with the problem of "lumping" the various entities in a few long-recognized species and thereby concealing the problem, or of recognizing more taxa in an attempt to at least pose some of the problems in the group. I shall follow the latter course. It seems clear that there is a New World and an Old World facies in the genus as evidenced in the tendency towards reduction of the calyx in the 3-merous species of the New World. Furthermore the fact that in some 3-stamen species the stamens are opposite the carpels and in others alternate, but never are they opposite the petals, suggests marked instability in the number of whorls of stamens in the genus. Because of the above problems we find no evidence to support the reference of our 3-merous species to the European *E. triandra* as has long been the practice. This latter species has a regular 3-merous calyx with all sepals very small in proportion to the corolla. Our plants which have in the past been referred to *E. triandra* all have 2 large oblong sepals often equalling the corolla in length and the third much reduced or absent. On the other hand the introduced rice field weed, *E. ambigua,* has three regular sepals. Field study of the group makes one suspicious that both apomixis and cleistogamy have operated to complicate the pattern of variation. This needs investigation. I have found nothing referrable to *E. americana* in California.

Elatine gracilis sp. nov. Plantae graciles erectae 2–4 altae foliis oppositis subaequalibus vel internodia paulo excedentibus ad bases petiolis similes angustatis stipulis laceratis attenuatis instructis flore nodo quoque unico sessili sepalis duo tertio reducto vel deficiente petalis tribus membranaceis fere orbicularibus staminibus tribus vel uno vel nonnumquam deficientibus carpellis alternantibus seminibus rectis vel paulo curvatis in loculo quoque 7–8 areolarum ordinibus 9–10 areolis in ordine unoquisque 20–30 partibus testae elevatis horizontalibus infra areolarum ordines manifestioribus quam eis longitudinalibus habitu plantarum aquatilum terrestriumque simili.

Plants slender, erect, 2–4 cm. high; leaves opposite, subequal to slightly longer than internodes, narrowed to a petiole-like base with attenuate lacerate stipules; flowers 1 to a node, sessile; sepals 2, a third sepal reduced or wanting; petals 3, thin membranous, almost orbicular, stamens 3–1 or sometimes none, alternate the carpels; seed straight to slightly curved, 7–8 per locule, the areolae in 9–10 rows, 20–30 areolae in each row; the horizontal ridges more conspicuous than longitudinal; aquatic and terrestrial plants similar in habit.

Type. Terrestrial; 0.4 mile south of Little Truckee River Bridge on Hiway 89, altitude ca. 6300 feet, Sierra County, California, 17 August 1952, *Herbert L. Mason 14,494* (UC 985951).

Elatine heterandra sp. nov. Plantae procumbentes foliis oppositis 2–4 mm. longis obovatis vel oblongo-ellipticis stipulis hyalinis lanceolatis ca. 1 mm. longis floribus nodalibus solitariis inter se alternantibus trimeribus staminibus 3–6 ac quando 3-carpellis oppositis seminibus in loculo quoque 8–12 rectis vel curvatis ad apicem versus rotundatis hilo truncatis apiculatisque areolis in ordinibus 9–10 positis in ordine quoque 12–15.

Prostrate plants, leaves opposite, 2–4 mm. long, obovate to elliptic-oblong; stipules hyaline, lanceolate about 1 mm. long; flowers solitary at nodes and alternate one another, 3-merous, stamens 3–6 when 3 opposite carpels; seed 8–12 per locule, straight or curved, rounded above, truncate and apiculate at hilum, areolae in 9–10 rows, 12–15 in each row.

Type. Pond, 1.5 miles east of Calpine at junction of Calpine with Sierraville-Beckwourth road, altitude ca. 5000 feet, Sierra Valley, Sierra County, California, 19 July 1952, *Herbert L. Mason 14,450* (UC 985952), topotype, *Mason 14,448;* Snow's Lake, Lake County, California, *Mason 14547.*

Elatine obovata (Fassett) comb. nov. *Elatine triandra* var. *obovata* Fassett, Rhodora 41: 375. 1939.

Elatine obovata has been treated by Fassett as a variety of the European *E. triandra.* It seems more closely rleated to *E. brachysperma* in seed character while the size and shape of the leaves and the pattern of distribution clearly set it apart from that species.

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